The melobesioid alga *Mesophyllum engelhartii* (Rhodophyta, Corallinaceae) in South Africa

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Mesophyllum engelhartii is a crustose coralline, melobesioid, red alga that is common in the Western Cape province and parts of the Eastern Cape province but becomes rare in KwaZulu-Natal. It occurs mainly on rocks and shells in the low intertidal and subtidal zones. The principal characters defining the species are the slightly to markedly prominent conceptacles and the structure of the tetra/bisporangial pore plate that is composed (in vertical section) of 4–6 somewhat elongate cells that are similar throughout and not specialized either in the conceptacle rim or in cells adjacent to pores.

The following type specimens, described by Foslie on the basis of South African material, are shown to be conspecific with *M. engelhartii*: the lectotype and isolectotype of *Lithothamnion discrepans*, and the holotype of *Lithothamnion synanablastum* f. *speciosa*. The isotype of *Goniolithon elatocarpum* is probably also conspecific but bears only non-diagnostic carposporangial conceptacles. As the epithet *engelhartii* has nomenclatural priority, the other taxa are now subsumed in *Mesolphyllum engelhartii* which is a common southern Australian species.

Mesophyllum engelhartii is 'n korsagtige melobesoïede rooi alg wat algemeen voorkom in die Wes-Kaap en dele van die Oos-Kaap, maar skaars is in KwaZulu-Natal. Dit kom grotendeels voor op rotse en skulpe in die lae intergety- en subgety-gebiede. Die belangrikste kenmerke wat die spesie definieer, is die effens tot duidelik prominente konseptakulums en die struktuur van die tetra/bisporangiale porieplaat wat in lengtesnee saamgestel is uit vier tot ses effens verlengde selle. Hierdie selle is deurgaans dieselfde en is nie gespesialiseer in die konseptakulumrand of in die selle aangrensend tot die porieë nie.

Die volgende tipe-eksemplare, beskryf deur Foslie op Suid-Afrikaanse materiaal, is konspesifiek met *M. engelhartii*: die lektotipe en die isolektotipe van *Lithothamnion discrepans*, en die holotipe van *Lithothamnion synanablastum* f. *speciosa*. Die isotipe van *Goniolithon elatocarpum* is waarskynlik ook konspesifiek, maar dit dra slegs nie-diagnostiese karposporangiale konseptakulums. Omdat die epiteton *engelhartii* oor nomenklatoriese prioriteit beskik, word die ander taksa nou ingesluit in *Mesophyllium engelhartii* wat 'n algemene Suid-Australiese spesie is.

Keywords: Taxonomy, Rhodophyta, Corallinaceae, Melobesioideae, *Mesophyllum*, South Africa.

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Introduction

A study is being made of the taxonomy of South African non-geniculate coralline algae (Rhodophyta, Corallinaceae) based on collections made by the authors, Richard E. Norris and other colleagues. Priority is being given to studying ecologically significant species [e.g. *Spongites yendoi* (Foslie) Y. Chamberlain (1993)] and new or otherwise taxonomically interesting species [e.g. *Pneophyllum amplexifrons* (Harvey) Chamberlain & Norris, (1994), and *Heydrichia woelkerlingii* Townsend *et al.* (1994)]. Historical information and a map including collection localities were presented elsewhere (Chamberlain 1993).

The present species was collected mainly on rocks and shells, in the low intertidal and subtidal zones.

The present species and type specimens of *Lithothamnion discrepans* Foslie, *L. synanablastum* f. *speciosa* Foslie and *Goniolithon elatocarpum* Foslie, all collected from South Africa, are investigated. The possible identity of *Lithothamnion synanablastum* Heydrich (1897) is discussed.

Materials and Methods

Collections were made in the Eastern Cape and Western Cape provinces and KwaZulu-Natal, South Africa. Data were obtained from type collections housed at TRH. Details of collecting methods, techniques used for optical and scanning electron microscopy and terminology used for thallus anatomy are as given by Chamberlain (1993). Thallus form terminology follows that of Woelkerling *et al.* (1993). Drawings were made on the basis of individual slide preparations. Detailed colour matching was made by comparison with drawings of Kornerup and Wanscher (1978). (VS – vertical section; ! – specimen seen; YMC 89/303, UWC 91/218 etc. are the authors' collection numbers.)

Observations

Mesophyllum engelhartii (Foslie) Adey 1970: 23.

Basionym: *Lithothamnion engelhartii* Foslie, 1900: 18.

Homotypic synonyms: *Lithothamnion engelhartii* f. *imbricata* Foslie, 1900: 19.

Lithothamnion patena f. *engelhartii* (Foslie) Heydrich, 1907: 223 (as *engelhardii*).

Heterotypic synonyms: *Lithothamnion synanablastum* f. *speciosa* Foslie, 1900: 11.

Lithothamnion engelhartii f. *umbonata* Foslie, 1900: 18.

Goniolithon elatocarpum Foslie, 1900: 23.

Lithothamnion fumigatum Foslie, 1901: 7.

Lithothamnion fumigatum f. *aucklandica* Foslie, 1905: 16.

Lithothamnion versicolor Foslie, 1907a: 3.

Lithothamnion discrepans Foslie, 1907b: 8.

Lithothamnion lemniscatum Foslie, 1907b: 11.

Lithothamnion speciosum (Foslie) Foslie, 1907b: 16.

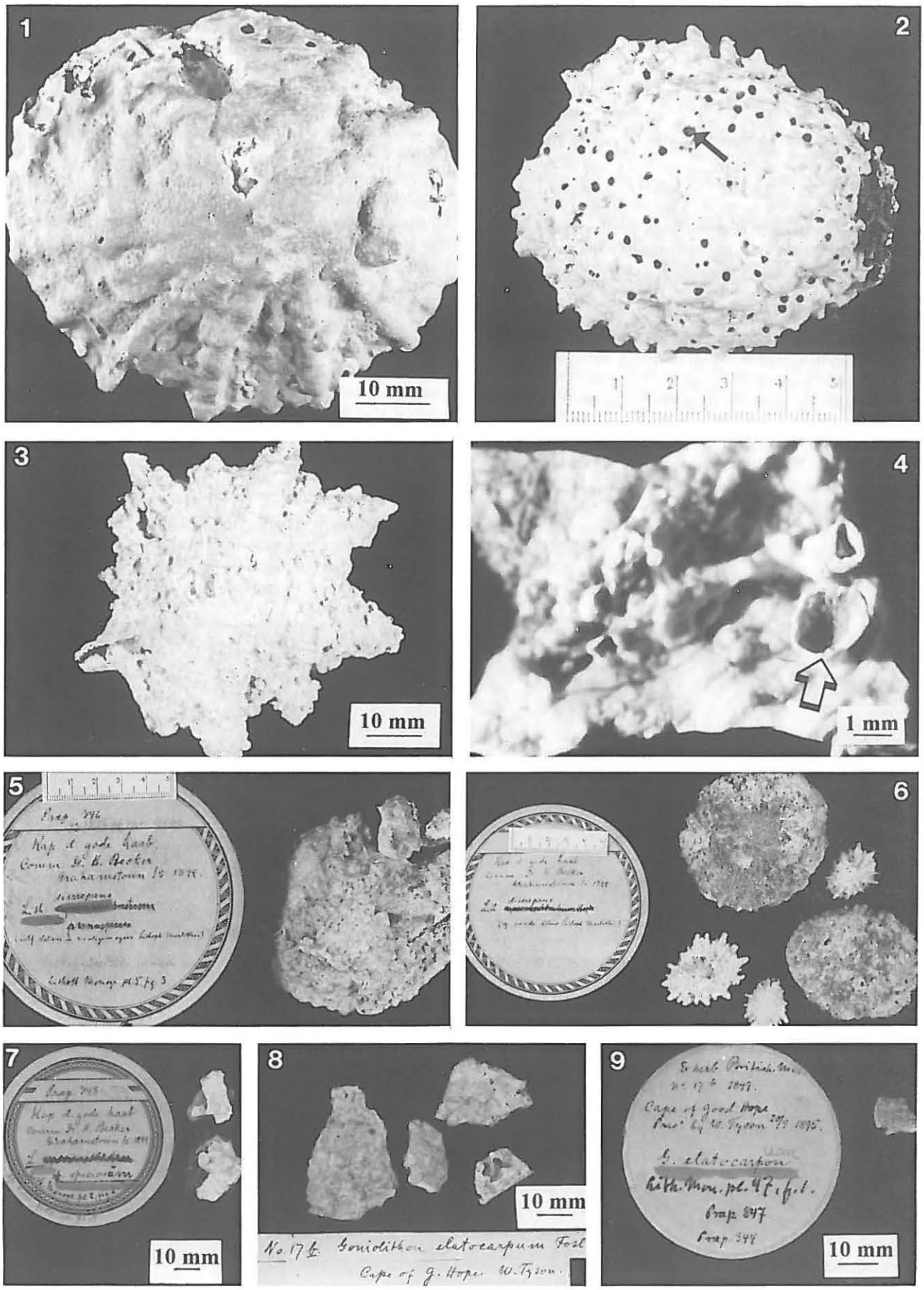
Lithothamnion aucklandicum (Foslie) Foslie, 1907b: 18.

Mesophyllum discrepans (Foslie) Lemoine, 1928: 252.

Mesophyllum aucklandicum (Foslie) Adey, 1970: 22.

Mesophyllum fumigatum (Foslie) Adey, 1970: 24.

Mesophyllum lemniscatum (Foslie) Adey, 1970: 25.



Figures 1–9 Habit of *Mesophyllum engelhartii* and appearance of relevant type specimens. **1.** Smooth thalli growing on *Patella barbara* (YMC 86/120). **2.** Thalli overgrowing turf-like algae on *Patella barbara*; the thallus is riddled with the colonial mollusc *Dendropoma corallinaceus* (arrow) (YMC 89/264). **3.** Frilly thalli on *Patella longicosta* (YMC 89/240). **4.** Under surface of holotype (TRH) of *Lithothamnion synanablastum* f. *speciosa* showing (arrow) 'cup-shaped rhizoids' (Foslie, 1900). **5.** Lectotype (TRH) of *Mesophyllum discrepans*. **6.** Isolectotype (TRH) of *Mesophyllum discrepans*. **7.** Holotype (TRH) of *Lithothamnion synanablastum* f. *speciosa*. **8.** Isotype (BM) of *Goniolithon elatocarpum*. **9.** Holotype (TRH) of *Goniolithon elatocarpum*.

Mesophyllum speciosum (Foslie) Adey, 1970: 26.
Mesophyllum versicolor (Foslie) Adey, 1970: 26.
Figures 1–56, Table 1.

Holotype: TRH. *Dr August Engelhart*, Cape Jaffa, South Australia.

Etymology: *engelhartii* honours the collector of the type specimen.

Distribution

SOUTH AFRICA: Common in Western Cape province and becoming occasional in Eastern Cape province. WORLD: Namibia, southern Australia, Auckland Islands.

Representative specimens examined

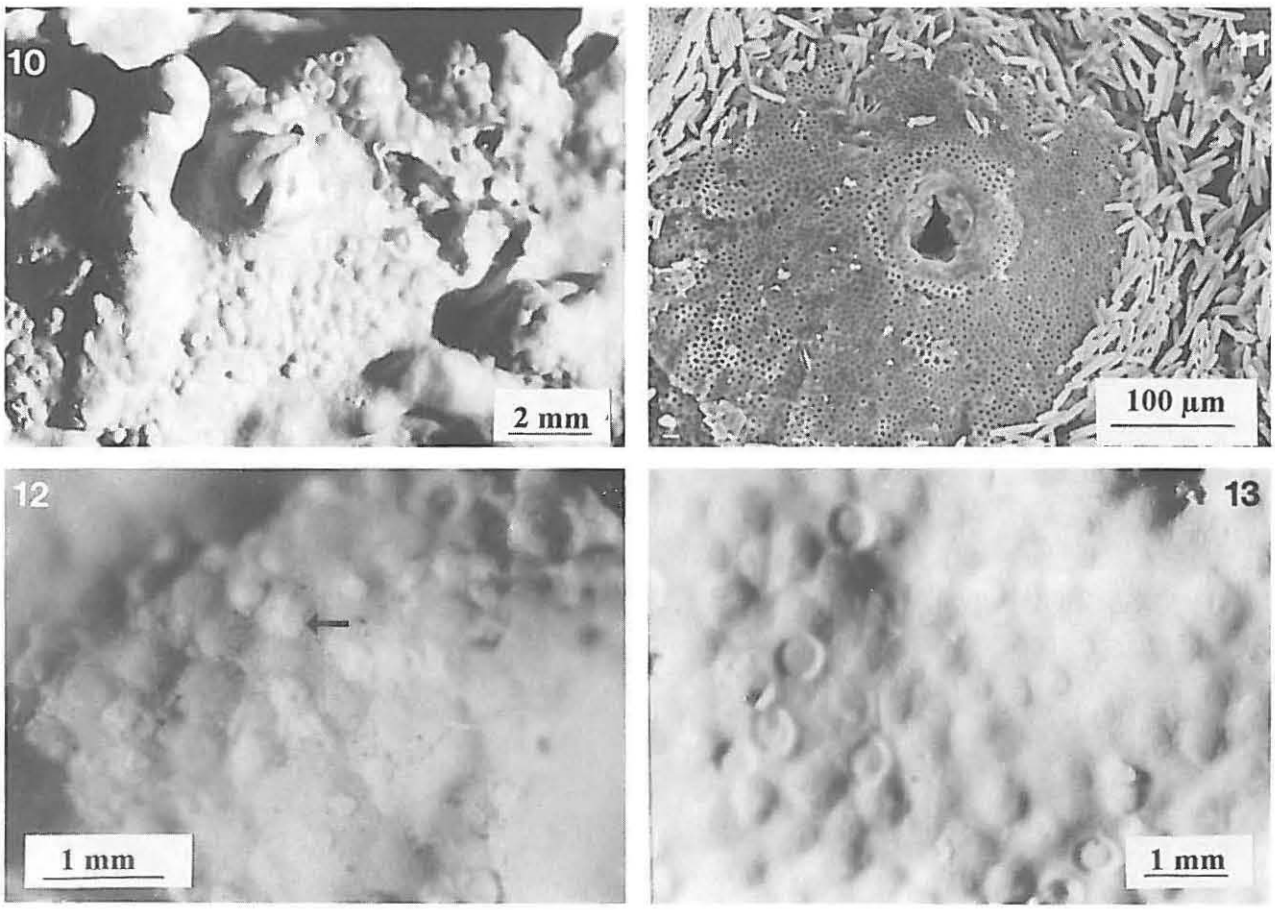
EASTERN CAPE: Cintsa, near East London, intertidal on rocks (*R. Anderson & J. Bolton*, vii.1987, YMC 89/205); Three Sisters, Port Alfred, on *Patella miniata* Born (*YMC*, 30.x.89, YMC 89/199); Skoenmakerskop, near Port Elizabeth (*YMC*, 3.x.1989, YMC 89/186). WESTERN CAPE: Cape Agulhas, littoral, on *Patella longicosta* Lamarck (*YMC*, 12.xi.1989, YMC 89/240); Brandfontein, on *Patella miniata* (*YMC*, 11.xi.1989, YMC 89/211); Cape of Good Hope, sublittoral on rock face (*YMC*, 14.xi.1989, YMC 89/251), littoral, on *Patella barbara* (*YMC*, 14.xi.1989, YMC 89/264); Oudekraal, Cape Peninsula, on *Patella barbara* Linnaeus (*R. Anderson*, 20.iv.1986, YMC 86/120; *RA*, 6.vi.1986, YMC 88/61), on *P. cochlear* Born (*RA*, 25.iii.1986, YMC 86/117; *RA*, 6.vi.1986, YMC 88/59); *RA*, 17.x.1986, YMC 88/72), and on rock at 5 m depth (*RA*, 3.x.1989, YMC 89/76); Bakoven, Cape Peninsula, sublittoral fringe, on *Patella barbara* (*RA*, 25.iii.1986, YMC 86/120); Holbaaipunt, SE of False Bay, on rocks and sabellarian tubes (*YMC & DWK*, 25.x.1991, YMC 91/80); Abdolsbaai, Paternoster, on *Patella granatina* Linnaeus (*YMC*, 29.xi.89, YMC 89/314 & 89/317); Doringbaai (*YMC*, 28.xi.89, YMC 89/294 & 89/304); Groenriviermond, on *Patella argenvillei* Krauss (*S. Eekhout*, vii.1989, YMC 89/274, 89/279 & 89/281).

Habitat and seasonality

Mesophyllum engelhartii is one of the commonest crustose coralline species on rocks and *Patella* shells (Figures 1–3) at low intertidal level where it forms mainly brownish thalli. It overgrows most other species of crustose coralline algae and *Pyrenocollema* lichens but is usually overgrown by *Heydrichia woelkerlingii* (Townsend *et al.* 1994). It is also common in the subtidal zone to at least 8 m depth, growing on stones, shells, *Ecklonia* holdfasts and rock faces on which it may form extensive, gleaming reddish-brown sheets. It is perennial and plants bearing abundant conceptacles were collected in March, April, May, July, October and November. Data are not available for other months.

Habit and vegetative structure

Measurements are mainly given in Table 1. Plants (Figures 1–3) are encrusting, adherent, and measure to at least 100 mm in diameter and 1.5 mm thick (more in protuberances). Thalli vary from flat to lumpy, to layered, with lamellae often overgrowing



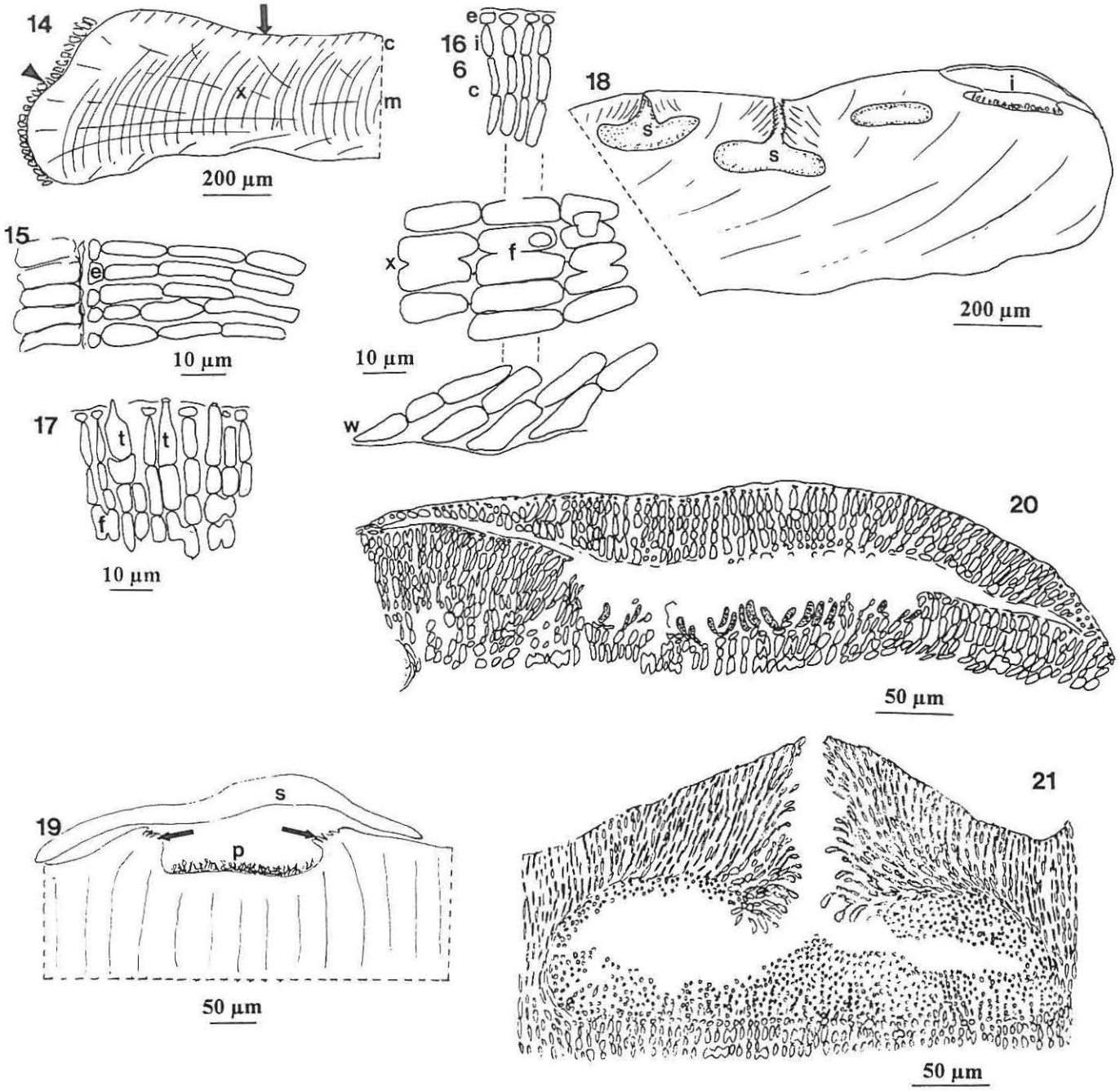
Figures 10–13 Features of gametangial and type specimens of *Mesophyllum engelhartii*. **10**. Gametangial thallus with crowded uniporate conceptacles (YMC 91/80). **11**. Gametangial conceptacle of smooth plant (YMC 86/120). **12**. Young tetrasporangial conceptacles shedding white discs (arrow) (TRH Holotype of *Lithothamnion synanablastum* f. *speciosa*). **13**. Gametangial conceptacles of smooth plant (YMC 86/120).

Table 1 Comparison of characters in *Mesophyllum engelhartii* from South Africa (SA) and southern Australia (sAus) (from Harvey and Woelkerling 1994); lectotype and isolectotype (TRH) of *Lithothamnion discrepans*; holotype (TRH) of *Lithothamnion synanablastum* f. *speciosa*; and isotype (BM) of *Goniolithon elatocarpum*. (Measurements are in micrometres unless stated otherwise)

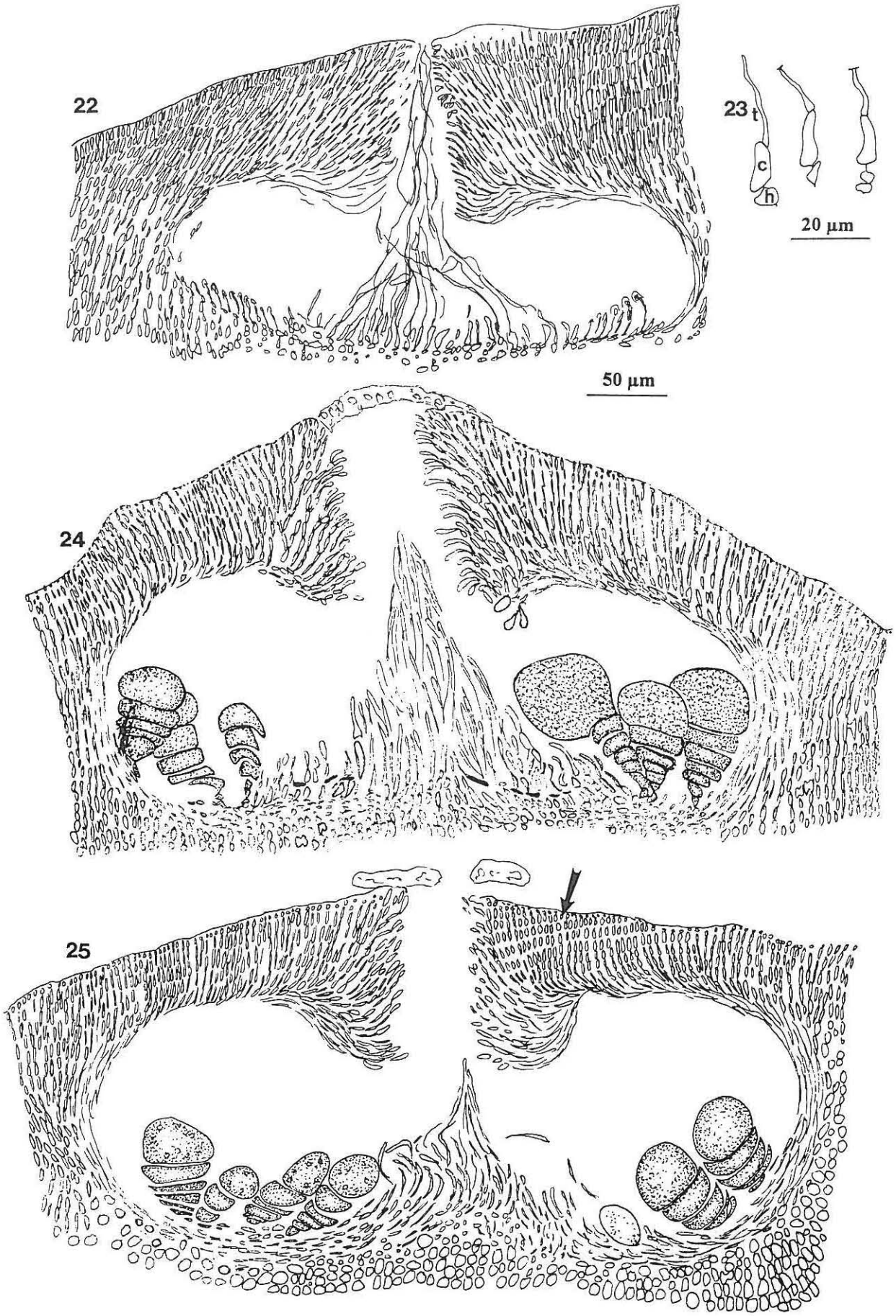
	M. engelhartii (SA)	*M. engelhartii* (sAus)	*L. discrepans*	f. *speciosa*	*G. elatocarpum*
Maximum thickness (dorsiventral thallus)	1.5 mm (excl. protuberances)	22 mm (incl. protuberances)	1.5 mm	520	>8 mm
Medulla					
Thickness	Up to 80%	—	Variable	Up to 80%	*ca.* 10%
Coaxial	From mainly to non-coaxial	From mainly to non-coaxial	Partly	Mainly	Non-coaxial
Cell length	11–50	16–33	11–33	20–46	15–28
Cell diameter	4–11	4–19	5–13	6–10	3–7
Cortex					
Cell length	5–20	9–14	5–20	6–16	7-20
Cell diameter	2–11	3–9	2–7	3–6	3–8
Epithallial cells					
Number	1	1	1(3)	1	1
Length	2.5–4	4–9	*ca.* 2.5	2–3	*ca.* 3
Diameter	2.5–5	3–5	*ca.* 5	3–5	*ca.* 5
Male conceptacle chamber					
Diameter	218–442	(54) 108–175 (284)	—	—	—
Height	52–104	21—108	—	—	—
Roof thickness	52–105	(32) 40–54 (135)	—	—	—
Carposporangial conceptacle chamber					
Diameter	286–520	189–500	—	—	*ca.* 540
Height	78–195	48–230	—	—	210
Roof thickness	65–130	100–180	—	—	120
Tetra/bisporangial conceptacle chamber					
Diameter	182–338	160–500	187–276	166–210	—
Height	104–208	65–260	109–187	145–150	—
Roof thickness	26–104	24–68	26–31	23–30	—
Number of cells in roof filaments	4–6	3–10	up to 6	4-6	—
Number of pores	up to 70	—	up to 60	—	
Number of cells surrounding pore (surface view)	5–9	—	*ca.* 7	*ca.* 7	—
Tetrasporangium					
Length	65–120	59–173	—	*ca.* 105	—
Diameter	23–104	24–81	—	*ca.* 60	—
Bisporangium					
Length	—	68–110	—	—	—
Diameter	—	22–65	—	—	—
Old conptacles becoming buried	Sometimes	Sometimes	No	No	Yes

one another (Figure 36) and/or regenerating on top of senescent thalli. Adjacent thalli often form crests where they meet. The thallus margin is entire, pale, often thickened, with strong orbital ridges and varies from strongly adherent to free and wavy. The colour is brownish (Methuen: brown or greyish brown) in positions exposed to insolation and deep mauvish brown to reddish (Methuen: dark to reddish brown, greyish to violet brown, or greyish to dark ruby) where more shaded. The thallus surface varies from smooth to roughened, the texture is matt to somewhat glossy. Cells in surface view (Figure 27) are *Phymatolithon*-type (Chamberlain 1990) and have calcified ridges encircling concavities.

Conceptacles are the same colour as the thallus and they occur over the entire surface except for marginal areas. Gametangial conceptacles (Figures 10, 11) vary from domed to conical, male ones are sometimes apiculate. Tetrasporangial conceptacles (Figures 26, 29) are rather inconspicuous to the naked eye, usually somewhat raised with a flat top and pale centre; the rim is apparent but not raised. The pore plate (Figures 28, 29) has up to 70 small pores, each is surrounded by 6–10 cells (Figures 28, 35)



Figures 14–21 Vertical sections of *Mesophyllum engelhartii*. **14**. Diagrammatic drawing of monomerous, coaxial (x) thallus edge; note cortex (c) and medulla (m) (YMC 89/281). **15**. Thallus margin at arrowhead in Figure 16; note epithallial cells (e) and senescent cells (s) attached externally to the margin. **16**. Representative cells through thallus at arrow in Figure 14; note epithallial cells (e), cortex (c), coaxial medulla (x) (arrow) with cell fusions (f) and lowermost edge of thallus (w). **17**. Upper thallus showing trichocytes (t) (YMC 89/251B). **18**. Diagrammatic drawing of thallus edge showing immature (i) and mature (s) male conceptacles (YMC 88/59). **19**. Diagrammatic drawing of immature male conceptacle showing shedding of outer thallus (s), growth of surrounding filaments (arrows) forming conceptacle roof, and protective cells (p) (YMC 89/314B). **20**. Young male conceptacle showing protective cells (shaded) (YMC 88/59). **21**. Mature, low conical male conceptacle with simple spermatangial systems all round (YMC 89/314B).



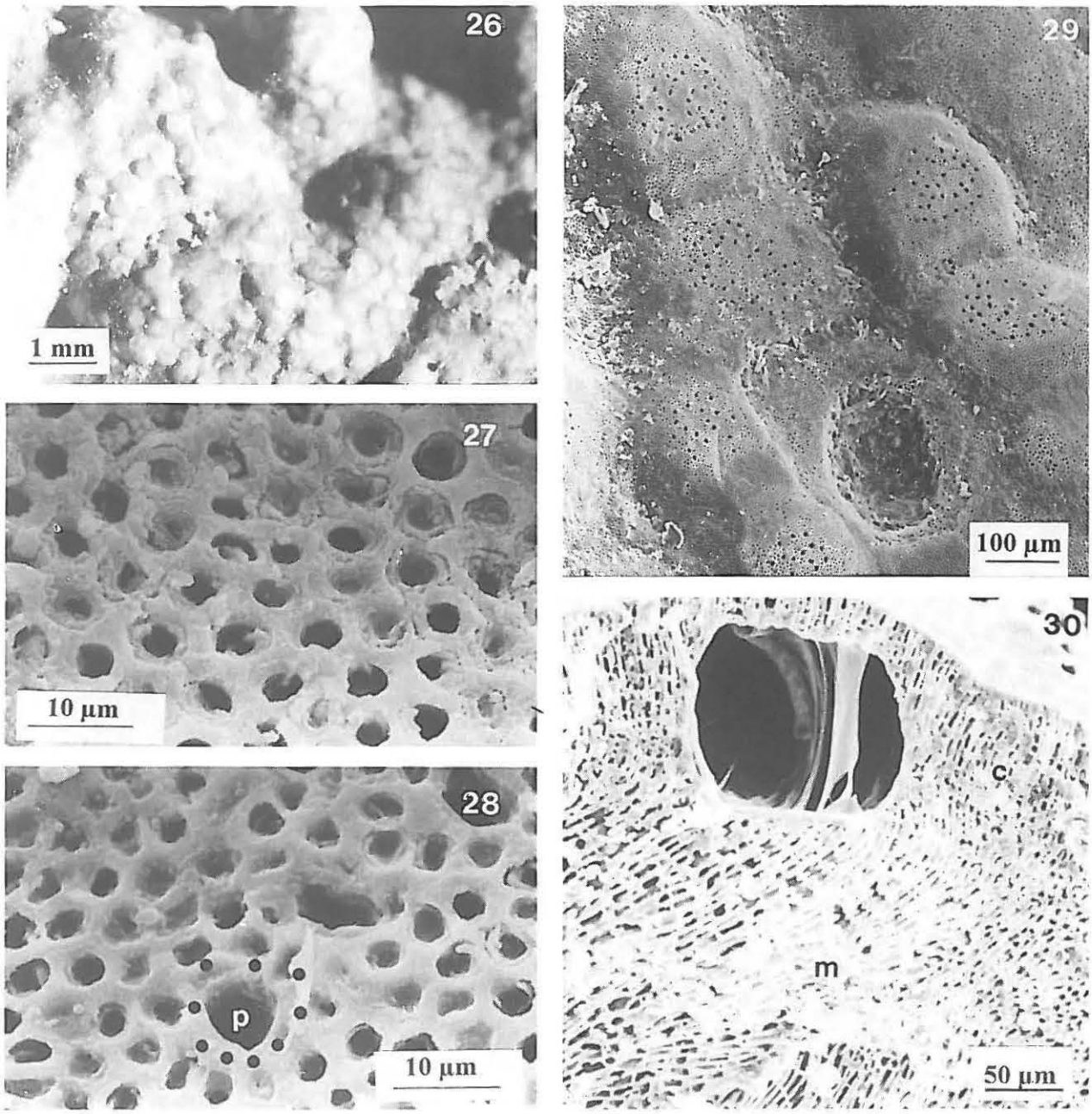
Figures 22–25 Vertical sections of carpogonial/carposporangial conceptacles of *Mesophyllum engelhartii*. **22**. Carpogonial conceptacle (YMC 88/61). **23**. Carpogonia from Figure 22 showing hypogynous cell (h), carpogonium (c) and trichogyne (t). **24**. Low conical carposporangial conceptacle; note possible discontinuous fusion cell (black shading) (YMC 89/314A). Scale as in Figure 22. **25**. Flush carposporangial conceptacle with horizontally aligned roof cells (arrow) (YMC 88/72). Scale as in Figure 22.

that are flush with, and do not differ from, other surface cells. The thallus (in VS) is monomerous (e.g. Figures 14, 31, 33). Filaments at the thallus margin (Figure 15), at least in part, terminate in epithallial cells. Apparently senescent cells occur on the thallus margin (Figure 15), the significance of which is unknown. The medulla composes up to 80% of thallus thickness; it is mainly or partly coaxial (Figures 14, 33) with elongate cells (Figure 16). Lowermost cells (Figure 14) are elongate and lack epithallial cells. The cortex is composed of elongate cells (Figure 16) that are sometimes markedly aligned horizontally. Cell fusions are present in the medulla and cortex (Figures 16, 17), secondary pit connections were not seen. Subepithallial initials (Figure 16) are elongate and as long as or longer than immediately subtending cells. Epithallial cells are single, varying from flattened and inconspicuous (Figure 16) to somewhat domed and distinct (Figure 32). Trichocytes (Figure 17) rarely occur.

Reproduction

Measurements are mainly given in Table 1. Gametangial plants are usually dioecious but sometimes monoecious. Male conceptacle chambers (Figures 18, 21) are low-elliptical. The roof is composed of more or less ascending filaments of long, thin cells; filaments surrounding the pore canal terminate in elongate papillae (Figure 21). Protective cells (Figures 19, 20) are present in young conceptacles. Spermatangial systems in mature conceptacles are simple (Figure 21) and borne on the floor, walls and roof of the conceptacle.

Carpogonial conceptacle chambers (Figure 22) are relatively



Figures 26–30 Tetrasporangial thalli of *Mesophyllum engelhartii*. **26**. Crowded tetrasporangial conceptacles (YMC 91/80). **27**. Thallus surface with calcareous ridges encircling epithallial concavities (UWC 91/220). **28**. Surface of pore plate showing pores (p) with nine surrounding cells (dots) (UWC 91/218). **29**. To show somewhat raised conceptacles, note pore plates (UWC 91/218). **30**. Vertical fracture of tetrasporangial conceptacle; note cortex (c) and medulla (m) (YMC 91/80).

wide and shallow; carpogonial branches (Figure 23) comprise a hypogynous cell bearing a single carpogonium extending into a trichogyne. After presumed karyogamy, carposporophytes develop in the carpogonial conceptacle chamber. The mature carposporangial conceptacle chamber is elliptical (Figures 24, 25) with roof development and structure as in male conceptacles. Senescent carpogonia (Figures 24, 25) occur in the centre of the conceptacle floor, no central fusion cell is present but discontinuous fragments (Figure 24) occur. Gonimoblast filaments (Figures 24, 25) are prolific. They develop peripherally and comprise up to six cells plus an enlarged, terminal carposporangium.

Tetrasporangial conceptacle chambers (Figures 30–34) are elliptical. The pore plate (Figures 32, 34) is up to 6 squarish to elongate cells thick; cells adjacent to pores and those at the periphery do not differ from other cells of the pore plate. Tetrasporangia (Figures 31–34) are elongate and zonately divided.

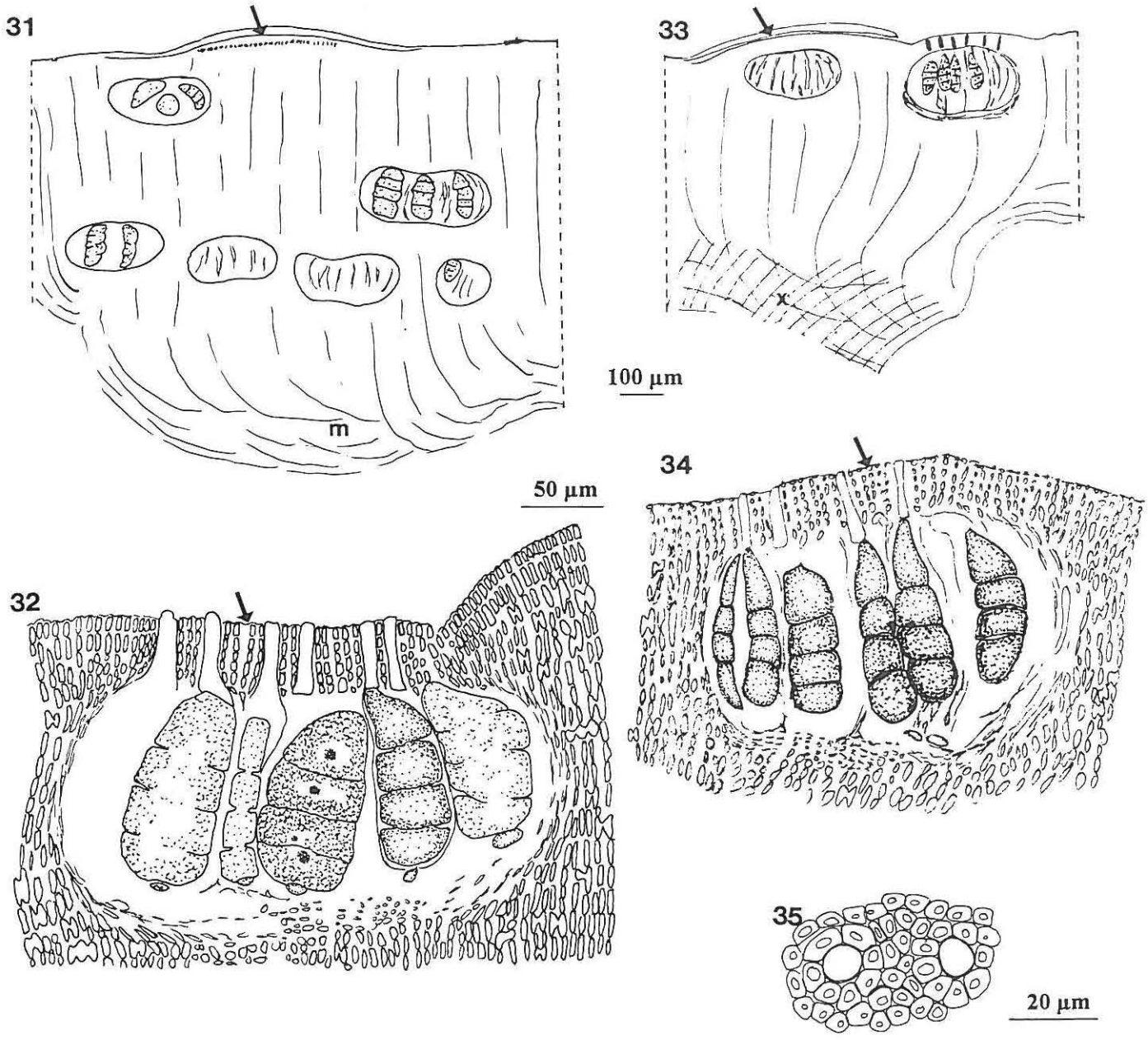
Most thalli lack buried conceptacles (Figures 18, 33), but some thalli occur with layers of buried conceptacles (Figure 31) that are mainly senescent but sometimes contain apparently normal carpogonia or other reproductive bodies.

Historical specimens

Lithothamnion discrepans Foslie 1907b: 8.

Lectotype: TRH! Grahamstown [presumably referring to the shores of Algoa Bay], South Africa, *H. Becker*, May 1899 [on *Patella tabularis* Krauss]. Printz 1929, Pl. V, Figure 3 (see Adey 1970: 23). Figures 5, 36–45; Table 1.

Isolectotype: TRH! Grahamstown, South Africa, *H. Becker*, May

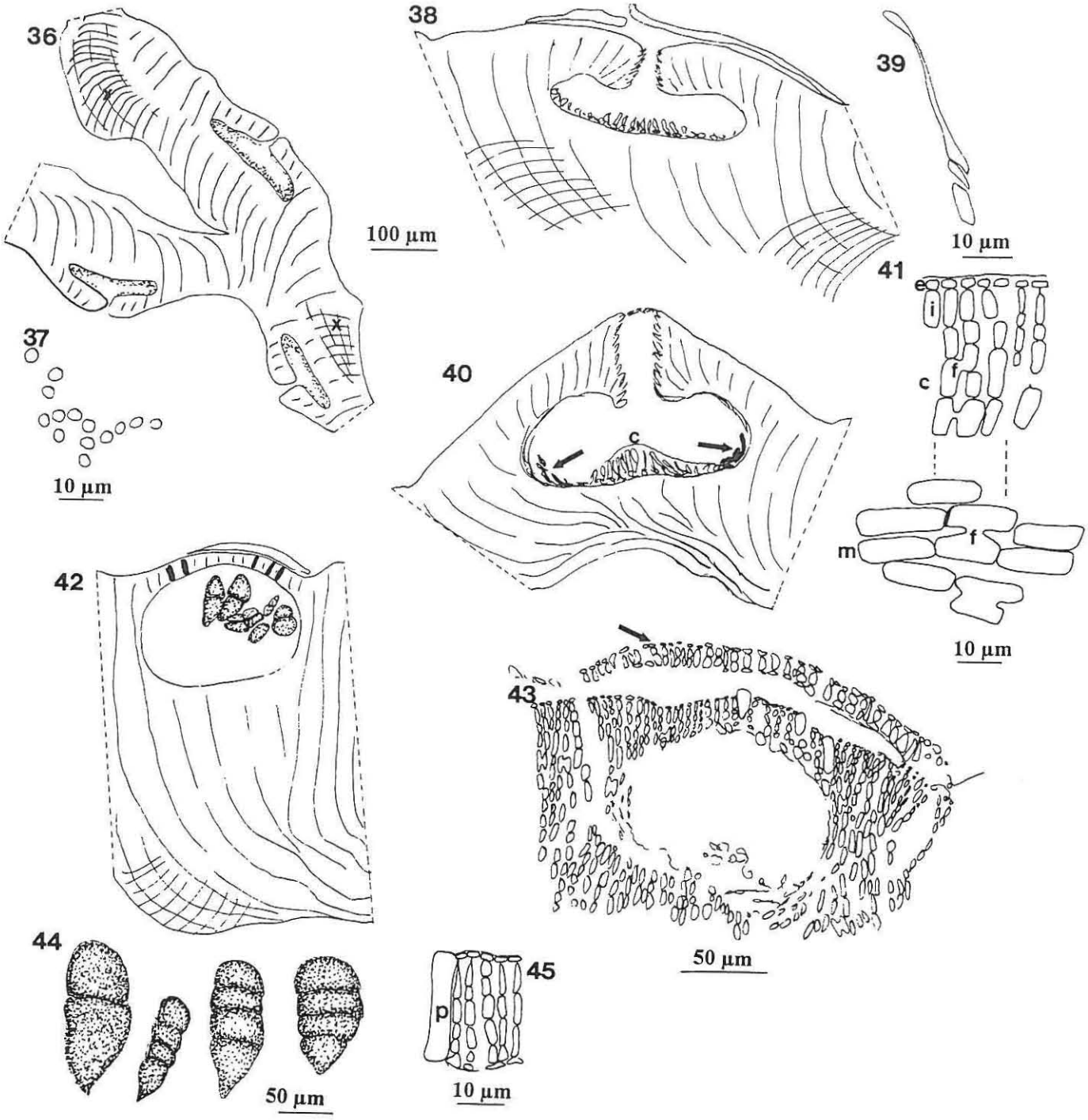


Figures 31–35 Vertical sections (except Figure 38) of tetrasporangial thalli of *Mesophyllum engelhartii*. **31**. Diagrammatic drawing of thallus with non-coaxial medulla (m) and immersed conceptacles, note conceptacle initiation (arrow) (YMC 86/120A). **32**. Mature flush conceptacle from thallus in Figure 34; note elongate, more or less aligned pore plate cells (arrow). **33**. Diagrammatic drawing of thallus with coaxial areas (x) in the medulla; note young conceptacle shedding upper thallus (arrow) (YMC 89/264). **34**. Slightly domed conceptacle; note small, unaligned pore plate cells (arrow). **35**. Surface view of tetrasporangial pore plate (YMC 89/264).

1899 [on *Patella tabularis*]. Figures 6, 39–43; Table 1.

Etymology: *discrepans* means differing, Foslie's (1907b) description provides no obvious explanation for the choice of this epithet.

There are two boxes (termed lectotype and isolectotype above) pertaining to *L. discrepans* in Foslie's collection. Adey (1970) designated as lectotype the collection relating to Foslie's slides 346 and 1556 (Figure 5); this was also the collection illustrated by Printz (1929, Pl. V, Figure 3). Woelkerling (1993) redesignated this specimen as holotype, but, as a choice had to be made between two specimens, Adey's (1970) designation is accepted here. The second specimen (Figure 6) is now considered to be an isolectotype.



Figures 36–45 Vertical sections of type specimens (TRH) of *Lithothamnion discrepans*. **36**. Diagrammatic drawing of male thallus of isolectotype showing regenerating lamellae and male conceptacles; note coaxial medullary areas (x). **37**. Released spermatangia from Figure 39. **38**. Diagrammatic drawing of carpogonial conceptacle from isolectotype. **39**. Carpogonium from isolectotype. **40**. Diagrammatic drawing of carposporangial conceptacle from isolectotype showing carpogonial remnants (c) and early gonimoblast filament (arrows). **41**. Representative thallus cells from lectotype showing epithallial cells (e), subepithallial initials (i), cortex (c), medulla (m) and cell fusions (f). **42**. Diagrammatic drawing of lectotype thallus with bisporangial conceptacle. **43**. Tetrasporangial conceptacle from lectotype thallus; note surface shedding (arrow). **44**. Released tetra/bisporangia from lectotype thallus. **45**. Tetrasporangial pore (p) and pore plate filaments from lectotype.

Thalli of the lectotype (Figure 5; Table 1) overgrow a low-growing assortment of plants and animals that, in turn, grow on the shell of *Patella tabularis*. They comprise three adjacent, strongly adherent tetrasporangial thalli that are irregularly warty to lumpy. The plants variously coalesce to form crests up to *ca.* 3 mm high. Inconspicuous tetrasporangial conceptacles are scattered over the surface. They shed a thin calcareous disc when young and are apparently infilled when old.

Thallus and tetra/bisporangial conceptacle structure (Figures 41–45) and dimensions (Table 1) compare closely with present populations of *Mesophyllum engelhartii* from South Africa. Conceptacle contents are mostly tetrasporangia (Figures 42, 45) but bisporangia sometimes occur in the same conceptacles.

The isolectotype (Figure 6) comprises two shells of *Patella tabularis* bearing gametangial thalli of *M. engelhartii*, together with small shells of *Patella longicosta* bearing other crustose coralline species such as *Spongites yendoi* (Foslie) Y. Chamberlain. The structure and dimensions (Table 1) of the uniporate male (Figures 36, 37) and carpogonial/carposporangial (Figures 38–40) conceptacles compare well with present populations of *Mesophyllum engelhartii,* and the observed presence of protective cells in male conceptacles further confirms the generic attribution.

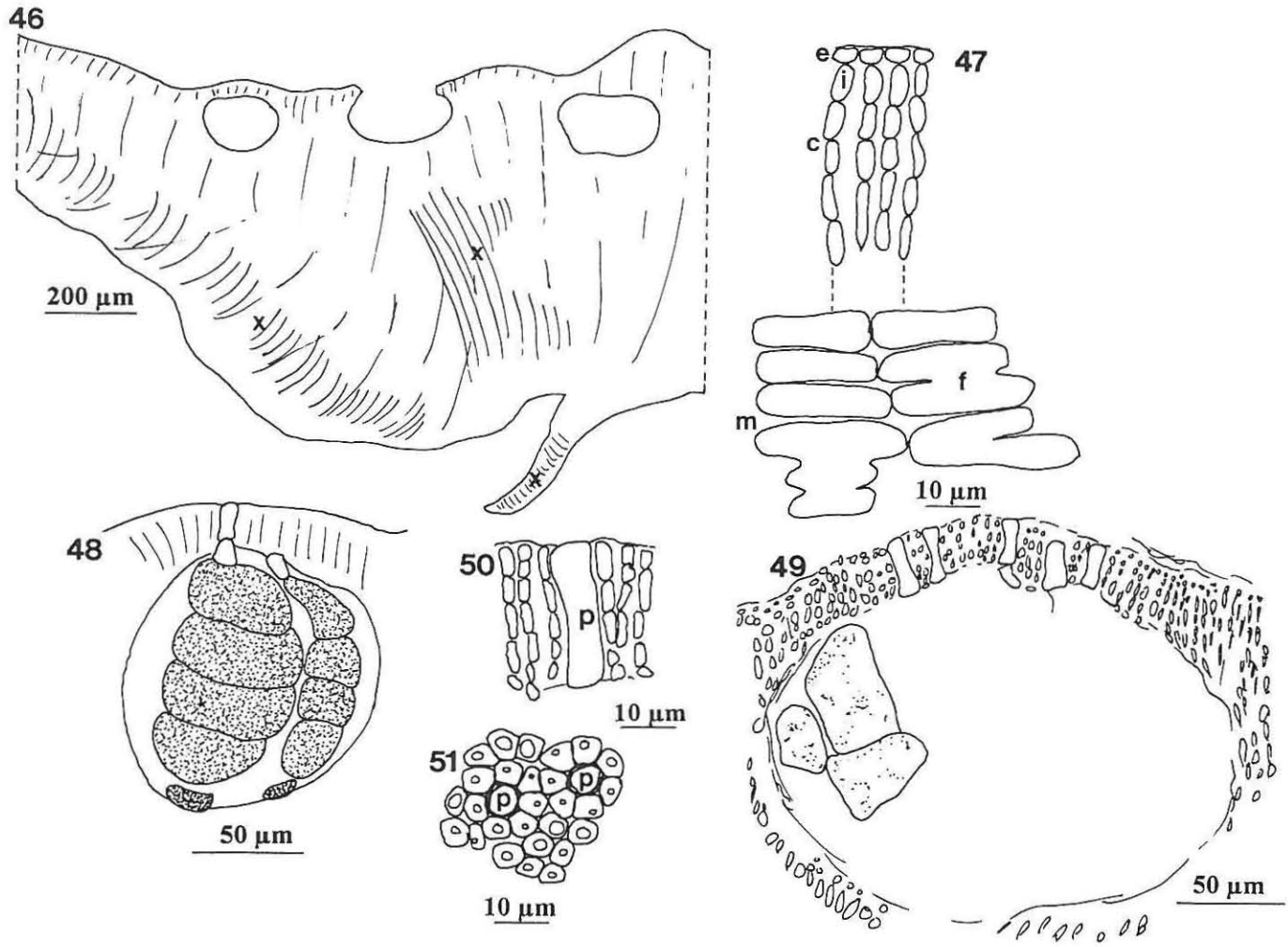
Lithothamnion synanablastum* f. *speciosa Foslie 1900: 11.

Holotype: TRH! Grahamstown, South Africa, *H. Becker*, May 1899 [growing on an algal ball]. Printz 1929, Pl. VIII, Figures 2, 3 (as *L. speciosum*). Figures 4, 7, 12, 46–51); Table 1.

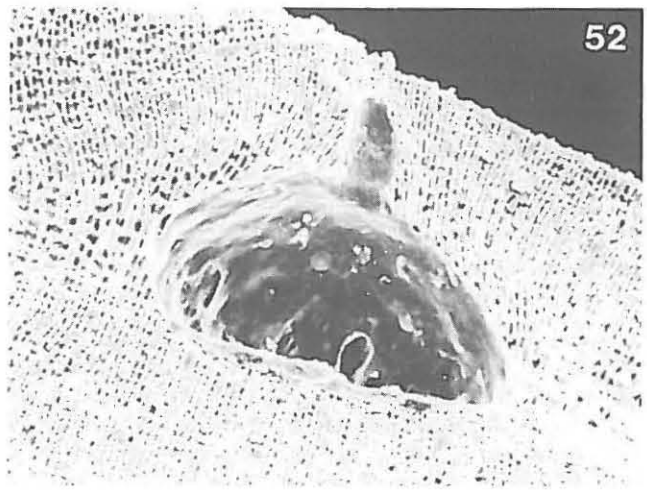
Etymology: *syn* – with; *ana* – growing upwards together; *blast* – shoot; Heydrich (1897) was presumably conveying what he described as the coalescent nature of the thalli; *speciosa* – splendid. It is difficult to understand why Foslie gave this name to a rather insignificant plant although he described it as growing in dense tufts and having cup-shaped rhizoids (Figure 4).

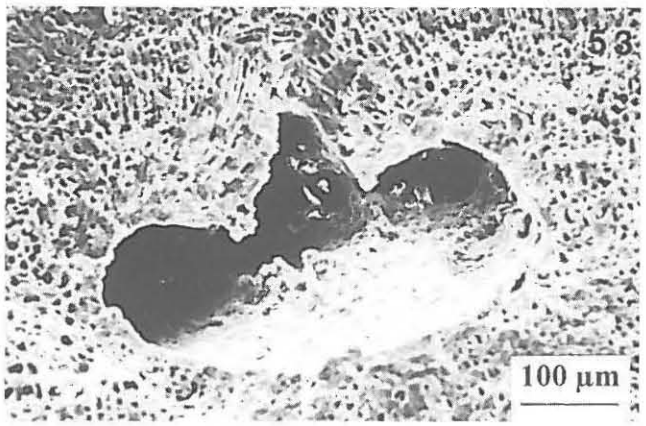
The general structure (Figure 46), coaxial medulla (Figure 47) and dimensions (Table 1) of the thallus and tetra/bisporangial conceptacles (Figures 46, 48, 49) of the holotype all compare well with present populations of *Mesophyllum engelhartii*. The thalli were growing on a soft plant mass resembling a *Cladophora* ball. The 'cup-shaped rhizoids' (Figure 4) are regenerative areas of lower thallus growth that attach the plant to the unstable substratum.

Foslie's (1900) description of this taxon as a form pertaining to *Lithothamnion synanablastum* Heydrich (1897) raises the problem of the identity of Heydrich's species. Based on Heydrich's (1897) description and illustration, together with Foslie's frequent mention of the species (see Woelkerling 1984), it is possible that *L. synanablastum* is conspecific with *Mesophyllum*

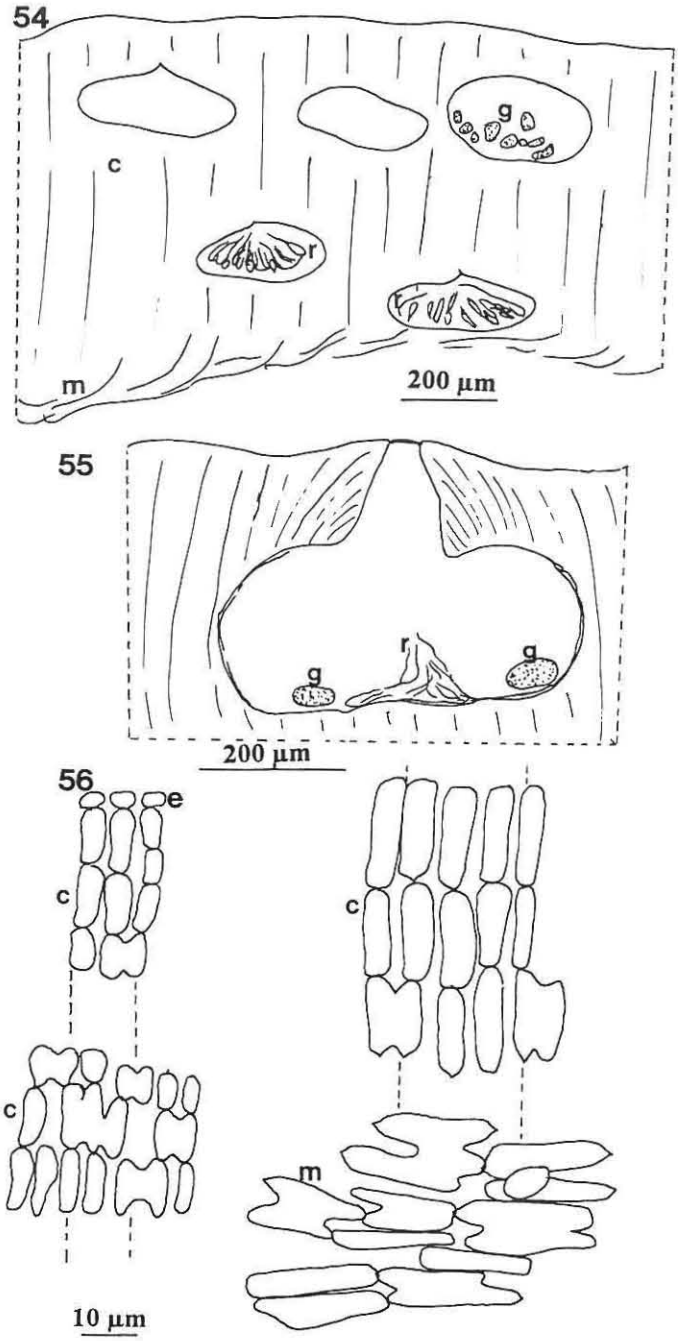


Figures 46–51 Vertical sections (except Figure 51) of holotype (TRH) of *Lithothamnion synanablastum* f. *speciosa*. **46**. Diagrammatic drawing of tetra/bisporangial thallus, note areas of coaxial (x) medulla. **47**. Representative thallus cells showing epithallial cells (e), subepithallial initials, cortex (c), medulla (m) and cell fusions (f). **48**. Edge of tetrasporangial conceptacle. **49**. Bisporangial conceptacle. **50**. Pore (p) and roof filaments from bisporangial conceptacle. **51**. Surface view of bisporangial pores (p).





Figures 52–53 Vertical fractures of isotype (BM) of *Goniolithon elatocarpum*. **52.** Thallus with carpogonial conceptacle. **53.** Buried carpogonial conceptacle.



Figures 54–56 Vertical sections of isotype (BM) of *Goniolithon elatocarpum*. **54.** Diagrammatic drawing of thallus showing cortex (c), shallow medulla (m) and buried conceptacles, some containing carpogonia (r) or carposporangia (g). **55.** Diagrammatic drawing of carposporangial conceptacle with carpogonial remnants (r) and remains of gonimoblast filaments (g). **56.** Representative cortical (c) and medullary (m) cells from various thallus levels.

engelhartii as now interpreted. Unfortunately, the type specimen was probably destroyed in Berlin during the 1939–45 war and crucial diagnostic characters such as the presence of protective cells in the male conceptacle and the structure of the tetrasporangial conceptacle roof cannot be confirmed.

The only known material identified by Foslie as *L. synanablastum* was collected by Mme Weber van Bosse at either Port Nolloth or Knysna (see Printz 1929, Pl. V, Figures 12–14). This material (TRH!) is now identified as *Synarthrophyton schmitzii* (Hariot) D. Keats & Y. Chamberlain (submitted). Foslie (1907c) also suggested that *Lithothamnion variabile* Foslie (1906) from the Falkland Islands was similar to *Lithothamnion synanablastum*. Unless the type of *L. synanablastum* is found, this species must be regarded as of uncertain status. Should type material be found and prove to be conspecific with *M. engelhartii*, the epithet *synanablastum* would have priority. The relationship of *Mesophyllum engelhartii* to *Lithothamnion variabile* needs to be investigated and is of particular interest in respect to the geographical distribution of species occurring in South Africa.

Goniolithon elatocarpum Foslie 1900: 23.

Holotype: TRH! Cape of Good Hope, South Africa, *W. Tyson*, 17b, 20.iv.1895. Figure 9.

Isotype: BM! Data as above. Figures 8, 52-56; Table 1.

The holotype is in TRH as noted by Adey and Lebednik (1967) and Woelkerling (1993). Woelkerling (1993) noted that only a small fragment of the specimen illustrated by Printz (1929, Pl. XLVII, Figure 1) was present in TRH. The main part of the specimen (see Tittley *et al.* 1984) (Figure 8) is in BM! and this material, now regarded as isotype, has been examined.

Etymology: *elato* – tall; *carpum* – fruit. Foslie may have been referring to the somewhat prominent uniporate conceptacles on this plant.

The low-lumpy plant (Figure 8) comprising the isotype, shows thallus (Figures 54, 56) and carpogonial/carposporangial (Figures 52, 53, 55) features and dimensions (Table 1) that agree with *Mesophyllum engelhartii* although the conceptacles differ some-

what in shape from those of *M. engelhartii* (Figures 22–25). In the absence of multiporate tetra/bisporangial conceptacles, this specimen could pertain to the Mastophoroideae. However, the habit and features appear to conform to those of the flatter type of *M. engelhartii* (Figures 1, 13) described below. This resemblance, together with the absence of any mastophoroid species with a similar thallus or carpogonia/carposporangia in the area, suggests that the species are conspecific, but some doubt must remain.

Discussion

The generic concept of *Mesophyllum* adopted by Woelkerling and Harvey (1993) is accepted here. As observed by Woelkerling and Harvey (1993) for southern Australian plants, *Mesophyllum engelhartii* is very variable in morphology and anatomy. South African plants show a similar range of forms except that epiphytic thalli, other than those extending from rock surfaces to *Ecklonia* holdfasts, have not been seen. One particular group of plants that encrust *Patella* shells (Figures 1, 13) are smoother and more matt than most other plants. Such thalli also have a preponderance of gametangial conceptacles and these and the tetrasporangial conceptacles are somewhat larger and flatter than usual. Additionally, contiguous cells of the cortex and roofs of all types of conceptacle are noticeably horizontally aligned (Figures 25, 32). This group could possibly be a distinct species or variety. However, a number of specimens could not be assigned confidently to either form and as plants from southern Australia with apparently similar features were assigned to *M. engelhartii* by Woelkerling and Harvey (1993, e.g. Figures 4D, 6A), we have taken the same action.

Conceptacle initiation (Figure 31) occurs in subepithallial initials and old outer thallus cells are shed (Figures 12, 19, 20, 31) as thin calcareous plates during conceptacle development. In male conceptacles, protective cells (Figures 19, 20) develop on the floor and are succeeded by simple spermatangial systems (Figure 21). No protective cells are seen to precede the simple spermatangial systems on the walls and roof of the conceptacle. Lebednik (1978) showed the presence of protective cells to be a diagnostic character of *Mesophyllum* and *Leptophytum* and protective cells have also been found (Harvey *et al.* 1994) in the genus *Synarthrophyton*. Woelkerling and Harvey (1993, Figures 8A, 8B) report, the presence of protective cells in *Mesophyllum engelhartii*. *Mesophyllum* differs from the other two genera in lacking any dendroid spermatangial systems on the conceptacle floor.

Each carpogonial filament consists of an hypogynous cell bearing a carpogonium and no sterile cells have been seen (Figures 23, 39). Suneson (1937, Figure 42g, as *Lithothamnion*) noted the same structure for the type species of *Mesophyllum*, viz. *M. lichenoides* (Ellis) Lemoine (1928). Carposporangial conceptacles bear prolific, peripheral gonimoblast filaments (Figures 24–25) in *M. engelhartii*. The nature of possible fusion cells is unclear. There is no central fusion cell, but scattered fragments of apparent fusion cells occur (Figure 24). Woelkerling and Harvey (1993) reported the presence of fusion cell complexes and possible discontinuous fusion cells in southern Australian *M. engelhartii*, and Figure 24 resembles their Figure 10C.

As has been discussed above, South African populations of *M. engelhartii* are considered conspecific with *Lithothamnion discrepans*, *L. synanablastum* f. *speciosa* and (probably) *Goniolithon elatocarpum*. In addition, five further taxa were included in synonymy by Woelkerling and Harvey (1993), as shown above.

Mesophyllum engelhartii is a common and very variable species in temperate regions of southern Africa and Australia; it also occurs in the sub-Antarctic on Auckland Island and the possibility of its presence in the Falkland Islands and southern South America needs investigation. The multiplicity of synonyms is typical of a very variable species. The species characteristics of *M. engelhartii* are:

(i) Plants encrusting, flat, to warty, to lumpy, to layered;
(ii) Margin often free and wavy, adjacent thalli often forming crests;
(iii) Medulla usually coaxial at least in part, often strongly so;
(iv) Male conceptacles fairly prominent, sometimes apiculate;
(v) Carposporangial conceptacles slightly to markedly prominent, gonimoblast filaments prolific, borne peripherally;
(vi) Tetra/bisporangial conceptacles somewhat raised, with more or less flat pore plate and up to 70 pores;
(vii) Tetra/bisporangial conceptacle roof composed (in VS) of 4–6 somewhat elongate cells that are similar throughout and not specialized either in the rim or in cells adjacent to pores.

A number of papers concerning melobesioid species from South Africa have been published (e.g. Chamberlain & Keats 1994; Keats & Chamberlain 1994) or are in preparation, and a key to the genera and species will be provided at a later date.

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References

ADEY, W.H. 1970. A revision of the Foslie crustose coralline herbarium. *K. norske Vidensk. Selsk. Skr.* 1970(1): 1–46.

ADEY, W.H. & LEBEDNIK, P.A. 1967. Catalog of the Foslie Herbarium. Det Kongelige norske Videnskabers Selskab Museet, Trondheim, Norway, 92 pp.

CHAMBERLAIN, Y.M. 1993. Observations on the crustose coralline red alga *Spongites yendoi* (Foslie) comb. nov. in South Africa and its relationship to *S. decipiens* (Foslie) comb. nov. and *Lithophyllum natalense* Foslie. *Phycologia* 32: 100–115.

CHAMBERLAIN, Y.M. & KEATS, D.W. (1994). Three melobesioid crustose coralline red algae from South Africa: *Leptophytum acervatum* (Foslie) comb. nov., *L. foveatum* sp. nov. and *L. ferox* (Foslie) comb. nov. *Phycologia* 33: 111–133.

CHAMBERLAIN, Y.M. & NORRIS, R.E. 1994. *Pneophyllum amplexifrons* (Harvey) comb. nov., a mastophoroid crustose coralline red algal epiphyte from Natal, South Africa. *Phycologia*, 33: 8–18.

FOSLIE, M. 1900. New or critical calcareous algae. *K. norske Vidensk. Selsk. Skr.* 1899(5): 1–34.

FOSLIE, M. 1901. New Melobesieae. *K. norske Vidensk. Selsk. Skr.* 1900(6): 1–24.

FOSLIE, M. 1905. Den botaniske Samling. *K. norske Vidensk. Selsk. Aarsberet* 1904: 15–18.

FOSLIE, M. 1906. Algologiske Notiser II. *K. norske Vidensk. Selsk. Skr.* 1906(2): 1–28.

FOSLIE, M. 1907a. Algologiske Notiser III. *K. norske Vidensk. Selsk. Skr.* 1906(8): 1–34.

FOSLIE, M. 1907b. Algologiske Notiser IV. *K. norske Vidensk. Selsk. Skr.* 1907(6): 1–30.

FOSLIE, M. 1907c. Antarctic and subantarctic Corallinaceae. *Wiss. Ergeb. Schwed. Südpolar-Exped.* 4 (5): 1–16.

HARVEY, A.S., WOELKERLING, W.J. & WILKS, K.M. 1994. The genus *Synarthrophyton* (Corallinaceae, Rhodophyta) in Southern Australia. *Phycologia* 33: 331-342.

HEYDRICH, F. 1897. Corallinaceae, insbesondere Melobesieae. *Ber. Dt. Bot. Ges.* 15: 34–71.

HEYDRICH, F. 1907. Über *Sphaeranthera lichenoides* (Ell. et Sol.) Heydr. mscr. *Beih. Bot. Cent.* 22: 234–238.

KEATS, D.W. & CHAMBERLAIN, Y.M. 1994. Two melobesioid coralline algae (Rhodophyta, Corallinaceae), *Mesophyllum erubescens* (Foslie) Lemoine and *M. funafutiense* (Foslie) Verheij from Sodwana Bay, South Africa. *S. Afr. J. Bot.* 60: 175–190.

KORNERUP, A. & WANSCHER, J.H. 1978. Methuen Handbook of Colour, 3rd ed., English Translation, 252 pp. Methuen, London.

LEBEDNIK, P.A. 1978. Development of male conceptacles in *Mesophyllum* Lemoine and other genera of the Corallinaceae (Rhodophyta). *Phycologia* 17: 388-395.

LEMOINE, Mme P. 1928. Un nouveau genre de Mélobésiées: *Mesophyllum. Bull. Soc. bot. Fr.* 75: 251–254.

PRINTZ, H. 1929. M. Foslie, Contributions to a Monograph of the *Lithothamnia*, pp. 60. Det Kongelige norske Videnskabers Selskabs Museet, Trondheim, Norway.

SUNESON, S. 1937. Studien über die Entwicklungsgeschichte der Corallinacean. *Acta Univ. Lund.*, N.F. Avd.2, 33(2): 1–101.

TITTLEY, I., IRVINE, L.M. & KARTAWICK, T. 1984. Catalogue of Type Specimens and Geographical Index to the Collections of Rhodophyta (Red Algae) at the British Museum (Natural History). Part 1. Corallinales, 64 pp (issued as a microfiche). British Museum (Natural History), London.

TOWNSEND, R.A., CHAMBERLAIN, Y.M. & KEATS, D.W. 1994. *Heydrichia woelkerlingii* gen. et sp. nov., a newly discovered non-geniculate red alga (Corallinales, Rhodophyta) from Cape Province, South Africa. *Phycologia*, 33: 177–186.

WOELKERLING, W.J. 1984. M.H. Foslie and the Corallinaceae: An Analysis and Indexes, 142 pp. (Bibliotheca Phycologica Vol. 69). J. Cramer, Vaduz.

WOELKERLING, W.J. 1993. Type collections of Corallinales (Rhodophyta) in the Foslie Herbarium (TRH). *Gunneria* 67: 1–289.

WOELKERLING, W.J. & HARVEY, A.S. 1993. An account of southern Australian species of *Mesophyllum* (Corallinaceae, Rhodophyta). *Austr. Syst. Bot.* 6: 571–637.

WOELKERLING, W.J., IRVINE, L.M. & HARVEY, A.S. 1993. Growth forms in non-geniculate coralline red algae (Corallinales, Rhodophyta). *Austr. Syst. Bot.* 6: 277–293.